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THE

SCIENTIFIC PROCEEDINGS

OF THE

ROYAL DUBLIN SOCIETY.

Vol. XV. (N.S.), No. 35. FEBRUARY, 1919.

A DISEASE OF TOMATO AND OTHER PLANTS CAUSED BY A NEW SPECIES OF PHYTOPHTHORA.

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(PLATES XLV.–XLVII.)

[*Authors alone are responsible for all opinions expressed in their Communications.*]

DUBLIN:

PUBLISHED BY THE ROYAL DUBLIN SOCIETY.

LEINSTER HOUSE, DUBLIN.

WILLIAMS AND NORGATE,

14, HENRIETTA STREET, COVENT GARDEN, LONDON, W.C.

1919.

Price One Shilling and Sixpence.

COMMONWEALTH MYCOLOGICAL INSTITUTE

Royal Dublin Society.

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XXXV.

A DISEASE OF TOMATO AND OTHER PLANTS CAUSED BY A NEW SPECIES OF PHYTOPHTHORA.

By GEORGE H. PETHYBRIDGE, B.Sc., Ph.D.,
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(Plates XLV.-XLVII.)

[Read November 19, 1918; published February 4, 1919.]

I.—Introduction.

In the early summer of 1916 specimens of diseased young tomato plants (*Lycopersicum esculentum* Mill.) were submitted from a nursery in the suburbs of Dublin to the Seeds and Plant Disease Division of the Irish Department of Agriculture for examination and report as to the cause of the malady and the possibility of curing or preventing it.

A preliminary examination of the specimens at once showed that the trouble was not due to any of the commonly occurring diseases of the tomato. On the contrary, the disease appeared to be one of a new type; and a visit was therefore paid to the nursery in question to examine further cases of it, and to obtain information concerning its origin and degree of seriousness.

It was learned that the disease was first noticed in this nursery three years previously, only a few plants being attacked at that time. In the succeeding year it had become more serious, while at the time of our visit nearly one-half of a large stock of young tomato plants were found to be either dead or dying. In these three years, therefore, the disease had become so well established in this particular nursery as to interfere very seriously with the raising of young tomato plants.

The same disease was discovered subsequently in two other nurseries, as well as in some private gardens in the same locality, while, during the course of our study of it, young tomato plants affected with it have been received from

various places in Ireland, showing that the disease must be fairly widespread here. We now have reason to believe that the disease also occurs in England.

Subsequent to the discovery of the parasite which causes the disease, cases of attack on Asters and Petunias by the same or a very similar organism were met with; and the scope of the investigation was extended to include such cases. Some account, therefore, of this part of our work is included in the present communication.

II.—Symptoms of the Disease.

The disease is usually first fully apparent when the young affected plants are about six inches high. In certain cases, however, it can be recognized in much younger plants, while in others the attack may not become obvious until the plants are considerably older.

It is characterized by the appearance of a brownish or blackish discoloration of the external tissues of the stem at or just above ground-level. These tissues become more or less shrivelled and destroyed, and sooner or later the top-heavy stem of the young plant falls over.

At first the foliage of the young plants does not usually show any characteristic symptoms of disease. Even on plants which have already toppled over, the leaves may remain green and turgid for a time, this being due to the fact that the upward passage of sap through the woody tissue of the stem is not all too seriously curtailed at the outset. As time goes on, however, the margins of the leaflets begin to roll upwards and inwards, the leaves turn yellow and finally die.

Occasionally, but not frequently, the foliage becomes flaccid or wilted before yellowing and death occur; but, strictly speaking, the disease is not one of the "wilt" type, and it is not one of hadro- or tracheo-mycosis such as occurs in tomato and potato plants when attacked by *Verticillium albo-atrum* (7).[1]

If an affected plant be lifted carefully from the soil, it is found that the rotting of the tissues at the base of the stem is continued downward into its underground portion and also into the root system. This, however, is the reverse of the direction in which the rot actually proceeds; for it starts in the roots, as a rule, works its way upwards for a short distance into the stem, and then usually ceases just above soil-level.

The cessation of the rot at this point is generally a decided one, and is perhaps due to changed moisture conditions. It may be stated here that if young plants which are not too far gone be cut off above the region of decay

[1] The figures in brackets refer to the bibliography at the end of the paper. See p. 503.

and be treated as "cuttings," many of them throw out a fresh set of adventitious roots, and develop into healthy, useful plants.

The primary root-system of an affected plant is usually badly decayed or entirely rotten. Evidently stimulated by the loss of these roots, the plant attempts to combat the attack of the parasite by developing a system of secondary, adventitious roots from the still healthy base of the stem higher up. But these also in turn become attacked; and finally the plant dies. It is, therefore, characteristic of this disease to see the older roots dead and decayed, and to find a bunch of adventitious roots formed above them, some of which may also be in process of being killed.

Essentially, then, the disease takes the form of a more or less rapidly progressing rot of the root system in which a portion of the base of the stem also becomes involved; and if a popular name for the disease be demanded, the term "tomato foot-rot" may, perhaps, be regarded as not unsuitable for it. A typically affected young plant is illustrated in fig. 1, Pl. XLV.

The rapidity with which death supervenes appears to be closely correlated with the age of the plant when first attacked; but it is doubtless also influenced by the conditions of temperature and moisture, both of soil and atmosphere, under which the plants are being raised. If infection occurs when the seedlings are young, death rapidly ensues; but if the plants are older, their struggle for existence is more prolonged.

On cutting the base of the stem of an infected plant longitudinally it is seen that the parts most involved in the rot are the soft parenchymatous tissues surrounding and surrounded by the wood. Microscopical preparations show the presence of comparatively abundant thin-walled, branched non-septate hyphae, of relatively large diameter, traversing these tissues both intra- and inter-cellularly. Where these hyphae invade still healthy tissue, however, they travel only between the cells. In very young seedlings hyphae of a similar kind were sometimes observed running longitudinally in the wood-vessels; but in older diseased plants the elements of the wood do not become invaded with hyphae until the rotting has reached an advanced stage.

Hyphae of the kind described are always found in the diseased tissues of affected plants; and if such plants are only recently attacked, these hyphae constitute practically the whole of the mycelium present. This mycelium, as will be seen from a subsequent section of this paper, was found to belong to a hitherto undescribed species of Phytophthora. Of course in later stages of the disease the dead tissues become invaded with saprophytic fungi and bacteria of various kinds; and these add considerably to the difficulty of making a satisfactory diagnosis of the actual parasite in advanced cases of the disease.

In one case at least a second parasite (a species of Pythium) was found along with the Phytophthora; but although in this particular instance the former may have contributed to the death of the plant, the detailed work carried out by us on numerous cases of the disease under consideration shows clearly that the real cause is not a Pythium but a Phytophthora.

III.—The Causative Parasite.

Specific proof that the fungus, to which the mycelium described above belongs, is the actual cause of the disease will be adduced in a later section of this communication. Before proceeding to this it will be desirable to give an account of the fungus and of its development on the host plant and in pure cultures.

Scrapings made from the superficial tissues of diseased stems below ground and examined with the microscope sometimes, but by no means always, show the presence of a few sporangia of a phycomycetous fungus of the Nozemia or the Phytophthora type. If affected plants be removed from the soil and allowed to remain in a moist atmosphere for a day or two, such sporangia are developed more freely. Better still, if the plants are placed with their roots and the bases of their stems in water, mycelium bearing these sporangia (but not in great abundance) grows out into the water from the diseased parts of the plant. This mycelium sometimes bears peculiar swellings such as are illustrated in fig. 9, Pl. XLVII., and these may be looked upon possibly as abortive attempts to produce sporangia or perhaps sexual organs. Some of them at any rate are suggestive of oogonial incepts which have not met with antheridia, but which, in spite of this, have made considerable growth. Similar bodies are also sometimes developed in pure cultures.

The sporangia are borne on sporangiophores which are branched in a sympodial manner. They are inversely pear-shaped, but often much elongated and somewhat irregular in form (fig. 2, Pl. XLVII.). The apex of the ripe sporangium is always blunt, but its wall in this region is always slightly thicker and more hyaline than elsewhere. In this respect the sporangium resembles that of *Phytophthora erythroseptica*, there being no apical papilla in either case such as is present in the sporangia of *P. infestans*. (See fig. 3, Pl. XLVII.)

The sporangia are rather firmly attached to the sporangiophores, and do not break off easily. When forcibly detached each sporangium carries with it a short length of the branch of the sporangiophore on which it was borne, which forms a very short stalk. The sporangium is filled with a granular mass of protoplasm. In size the sporangia vary considerably, ranging from 24μ to 50μ in length and 17μ to 30μ in breadth at the broadest part. On

the average they measure 40μ by 27μ, and they are, therefore, somewhat larger than those of *P. erythroseptica*.

The branches of the sporangiophores do not differ markedly from the ordinary mycelial hyphae, and are as a rule long and straggling. Careful observation has shown that the first formed sporangium is terminal, and that the branch of the sporangiophore which bears the second arises near the base of the first sporangium, which thus becomes pushed aside in the manner first described by de Bary for *P. infestans*, but no local swelling of the sporangiophore occurs, as in that species. More than three sporangia attached at one time to a branched sporangiophore have never been seen. (See fig. 4, Pl. XLVII.)

The mode of germination of the sporangia has been carefully followed, and it resembles very closely that occurring in *P. erythroseptica* (5). The contents of the sporangium become more coarsely granular, contraction of the contents from the sporangium wall occurs to some extent, and aggregation into a number of zoospore units takes place (fig. 3, Pl. XLVII.). Suddenly the thicker, hyaline, apical portion of the sporangium wall becomes stretched or expanded into an almost spherical, extremely thin-walled sac, into which the whole or the major portion of the contents of the sporangium immediately passes. Practically at the same moment the wall of this sac dissolves, and the contents of the sporangium break up into a number of zoospores which swim off in all directions. Any contents which may not have escaped from the sporangium become resolved at the same time into zoospores which may swim out of the now ruptured sporangium, or may remain within it and germinate there.

The zoospores are lemon-shaped with a distinct longitudinal groove on one side, from the base of which two cilia arise, one directed forwards and the other backwards. After a short time each zoospore comes to rest, loses its cilia, assumes a more or less spherical shape, secretes a thin wall and produces a germ-tube. When at rest the zoospores measure from 10μ to 15μ in diameter, and they are, therefore, somewhat larger than those of *P. erythroseptica*.

When a sporangium has liberated its zoospores it not infrequently happens that the branch of the sporangiophore which bore it grows directly onwards and forms a second sporangium. If this branch becomes elongated the second sporangium is formed outside of and beyond the original one, now empty, as is shown in fig. 7, Pl. XLVII. But if this branch remains short, the second sporangium, being almost sessile, remains within the first formed one; and a third may be developed within the second as illustrated in fig. 8, Pl. XLVII. A similar state of things has been described by Robinson (9) for

the fungus (presumably a Phytophthora, and possibly identical with the one now being dealt with) which causes the "Black Neck" disease of Asters.

Less commonly than by the production of zoospores the sporangium develops by producing a single germ-tube, which usually arises at the distal end of the sporangium (figs. 5 and 6, Pl. XLVII.). One very unusual case was observed, however (fig. 10, Pl. XLVII.), in which a single sporangium developed a considerable number of germ-tubes, one of which (much shorter than any of the others) proceeded from the usual place, while the others were distributed at various points over the surface. The appearance suggested that partial segregation into zoospore-units had occurred; the sporangium did not, however, open, and the free swimming stage of the zoospores was suppressed. Nevertheless, each zoospore-unit developed its own germ-tube, which grew out in the manner illustrated.

A very considerable amount of time and trouble has been spent in searching for the sexual organs of the fungus in the dead tissues of the host plant both when naturally infected as well as when artificially inoculated. What appear to be undoubted oospores of some fungus, frequently still surrounded by the remains of the oogonial wall, have occasionally been met with, but in no case has an antheridium been observed. These spores are somewhat smaller than those which are produced by the fungus when grown in pure culture; and they lack the yellowish tinge of the latter. They have a smooth, thick wall and granular protoplasmic contents, together with a large central oil drop, and a highly refractive body, probably containing the nucleus. They closely resemble, except in size, the ripe oospores of *Phytophthora erythroseptica.*

In most of the cases in which the attempt was made, these spores were successfully germinated, and the mode of germination in its early stages exactly resembles that described for the oospores of *P. erythroseptica* (5). When, however, the germ-tubes had reached a length equal to about three times the diameter of the spore, growth either ceased at once or soon after the formation of a terminal swollen body into which the contents of the germ-tube passed. In some cases this body sent out a germ-tube of its own which reached a length of several times that of its own diameter, and then ceased to develop further. In no case was mycelium, bearing sporangia of any sort, produced from these spores; hence it is not possible to say with certainty to what fungus they belonged.

Attempts were made to raise cultures from the germinating spores, but these failed, owing either to the early death of the germ-tubes or to serious contamination of the medium with bacteria; for it was naturally impossible to obtain these spores from the diseased host plant free from contamination.

The absence of antheridia might perhaps be explained by their becoming torn away during the process of teasing out the spores from the diseased tissues, but it seems scarcely probable that all signs of them would thus be obliterated. On the other hand, there is the possibility that the fungus may produce oospores in the tissues of the host parthenogenetically. *Phytophthora infestans* develops parthenogenetic oospores in pure cultures (8), and at least one other species described as a Phytophthora (*P. Theobromae*) produces oospore-like bodies or chlamydospores (?) in the tissues of the host it attacks.

The disease (as will be seen in a subsequent section of this paper) is contracted from the soil, and it is reasonable to suppose that oospores, or resting spores of some kind, are developed in the dead tissues of the host. We have, however, up to the present failed to obtain convincing evidence that this is the case. That true oospores are produced in pure culture will be evident from what follows in a later section (p. 496).

IV.—Proof of Pathogenicity.

Owing to the comparatively sparing production of sporangia and to failure to get the fungus to grow (except to a limited extent) from what possibly were its oospores, under conditions that could be controlled, it was found impossible to obtain the fungus in pure culture by starting from a single spore. It was, however, eventually isolated in the following way:—

Portions of diseased tomato stems, about one inch long, were steeped in a weak solution of mercuric chloride (1 : 1000) for one minute. After washing in sterile water and allowing to become air-dry, small portions of the inner affected tissues were removed with sterile instruments and under as aseptic conditions as possible to set plates of sterile media such as wort-gelatine, Quaker Oat-agar, and beef extract-agar.

After a few days, fungus mycelium had grown out from the portions of tissue to the surrounding medium, and fragments of the freshly grown peripheral mycelium were transferred with aseptic precautions to slants of Quaker Oat-agar in test tubes. Some of these transfers, after further growth had occurred, were found to be impure, being usually contaminated with bacteria. In a few cases, however, careful microscopical examination and the subsequent behaviour of the cultures clearly showed that a single organism was present; and parallel isolations showed that this organism was the same in all cases.

The organism thus isolated developed sporangia in culture similar to those found on the host plant. Its pathogenicity was proved in the following way:—Into the stems of each of two healthy tomato plants, grown in pots,

a small incised wound was made with a sterile scalpel at the region of soil-level, and into each wound a small portion of a six-day-old pure culture of the fungus was inserted. The wounds and their contents were then wrapped round with a bandage of tinfoil. A third plant was treated similarly, except that no inoculating material was placed in the wound; and this plant served as a control.

After the expiration of forty-eight hours it was clear that infection of the two inoculated plants had occurred, for rotting had set in beneath the tinfoil and had extended beyond it. Both plants had a tendency to fall over at the point of infection, and one of them was staked in order to prevent this. After a further two days the unstaked plant had fallen over and its lowest leaves were beginning to turn yellow. The upper part of the plant, however, was but little affected and had responded to the stimulus of gravity by carrying out a negatively geotropic curvature. In both plants the diseased areas had become shrivelled and brown, and they closely resembled naturally infected plants as seen in the nursery. The control plant showed no symptoms of disease throughout the experiment. These plants as seen four days after inoculation are illustrated in fig. 2, Pl. XLV.

A portion of the diseased tissue of one of the plants was incubated in a moist atmosphere, and the result was the production of a fair crop of sporangia exactly similar to those already described as being found on naturally infected plants. From the remaining portion the fungus was re-isolated by the method already described, and grown in pure culture; and it was found to be similar in all respects to that used for inoculation purposes.

This experiment clearly proved the pathogenic character of the fungus; and this has been confirmed by the results of very many inoculation experiments, subsequently carried out, in which failure to produce the disease has not once occurred. In plants which are older, infection following artificial inoculation occurs more slowly, but even in such cases the fungus ultimately obtains the mastery and the plants become killed.

Successful inoculation experiments were also made with tomato fruits, both green and when ripe. The fungus causes a rather rapid rot of the ripe fruit, accompanied by a most offensive odour. The type of rot produced is quite different from that described under the name of "Buckeye" rot by Sherbakoff (13), and due to *Phytophthora terrestria*. In one case—the only one where the attempt was made—the fungus was re-isolated in pure condition from an artificially rotted ripe tomato fruit, and proved to be identical with that used for the inoculation.

Infection experiments have also been carried out with various other plants. Negative results were obtained with *Senecio vulgaris*, *Helianthus annuus*, and

Nicotiana affinis. The fungus, however, was found capable of attacking Asters, Petunias, Wallflowers (Cheiranthus), *Gilia tricolor*, and seedlings of Beech (*Fagus sylvatica*), producing in all these plants symptoms very similar to those observed in naturally affected tomato plants. In some of these, as will be seen from a later section of this paper, the same disease occurs naturally.

When inoculated into living potato-tubers, the fungus causes a rot very similar to the "pink rot" caused by *Phytophthora erythroseptica.* When portions of the rotted tissue were placed in sterile water, sporangia were developed rather sparingly, but no sexual organs were formed. Under these conditions, *P. erythroseptica* produces an abundant crop of sexual organs and sporangia.

The fungus has been found to be actively parasitic to apples and white turnips. It also slowly attacks mangels and swedes, but does not attack carrots or parsnips. In all cases inoculation was carried out through wounds.

V.—Development of the Fungus in Pure Cultures.

The fungus was found to grow with more or less vegetative luxuriance on a considerable number of different agar and gelatine media, of which sixteen kinds were tried, as well as on sterilized portions of various stems, fruits, &c. It did not cause the liquefaction of gelatine media. The kind of mycelium developed is illustrated in fig. 1, Pl. XLVII.

The striking point about all these cultures was the reluctance of the fungus to produce either asexual or sexual reproductive organs. In a few cases, as, for instance, on sterile soil and on oat-extract-agar, there was a meagre development of sporangia. This also occurred when a small portion of a culture on Quaker Oat-agar was transferred to sterile tap-water or bog-soil-extract. In other cases, the addition of sterile water to tubes containing slanted cultures on various media resulted in a good development of mycelium in the water, but reproductive organs did not arise.

In the cases mentioned above in which sporangia were formed, they exactly resembled those already described both in shape and size as well as in method of zoospore production, and they need not, therefore, be described again.

At this point in our work the study of the fungus had to be suspended temporarily, owing to the pressure of urgent work more directly connected with food-production ; and a period elapsed during which the only thing done was to make transfers of the cultures every few weeks in order to keep the fungus alive and in good order until the study of it could be resumed. This period lasted from January to October. At the beginning of it the stock cultures were on Quaker Oat-agar, and this medium alone was used for the subsequent transfers. The whole series of original stocks and intermediate transfers was kept for future microscopical examination.

On resuming the work in October this examination revealed the abundant presence of sexual organs in the original stock cultures, which, however, at this time were dead; and these organs were also found in a few of the intermediate transfers, the more recent of which were still living. They were also produced, but not very abundantly, in sub-cultures made subsequently; and it was found that they developed rather more readily in a hard Quaker Oat-agar medium containing $12\frac{1}{2}$ per cent. of agar than in the one usually employed, which contains only $1\frac{1}{2}$ per cent. of agar.

The sexual organs are of the type first described for *Phytophthora erythroseptica* (4) and *P. infestans* (8). It is, therefore, clear that the fungus is a true Phytophthora. Using Murphy's (3) terminology the antheridia are amphigynous and not paragynous, as in the genus Nozemia.

The antheridium may be terminal or intercalary, and often has a short hypha proceeding from it, as in *P. erythroseptica*, which, as Murphy has suggested, may play the part of a safety-valve by relieving the pressure caused by the growth of the oogonial incept when within the antheridium. Ripe antheridia are variable in form and size, and their dimensions are not of much import for diagnostic purposes.

The oogonium may also be terminal, but it is more usually a lateral outgrowth. When ripe it is pear- or balloon-shaped. The oogonial incept having penetrated the antheridium and emerged from its top swells up to form an almost spherical sac in which the oospore is developed. The lower, funnel-shaped base of the oogonium remains within the antheridium and becomes closed at its narrow end with a cellulose plug. The rather thin wall of the oogonium is at first hyaline, but becomes amber-coloured with age. The average diameter of the spherical part of the oogonium is 30μ.

Fertilization probably occurs in the manner described by Murphy (3) for *P. erythroseptica*; and the oosphere develops into a thick-walled oospore, which, when ripe, contains a large oil drop surrounded by finely granular protoplasm in which a small oval highly refractive body lies which possibly contains the nucleus. The wall of the oospore, at first hyaline, becomes straw-coloured, and averages about 3μ in thickness, while the diameter of the spore averages 25μ. The germination of the oospores developed in pure cultures has not yet been followed. The sexual organs are illustrated in figs 3, 4, and 5, Plate XLV, and fig. 11, Plate XLVII.

VI.—Recognition of the Fungus as a New Species.

The peculiar morphology and mode of development of the sexual organs first discovered in *Phytophthora erythroseptica*, *P. infestans*, *P. Phaseoli*, and surmised to occur in *P. omnivora* var. *Arecae*, led to the suggestion (4), (6)

that the old genus Phytophthora should be divided. It was proposed that only those species with amphigynal antheridia should remain in this genus, and that the other species, with paragynal antheridia, formerly included in it, should be made to constitute a new genus, Nozemia. This suggestion has been followed by Murphy (3), who has recently published a detailed account of the morphology and cytology of the sexual organs of *P. erythroseptica*, but, unfortunately, not by Rosenbaum (11) in his statistical studies of species of the two genera. The latter author has, however, shown that the surmise as to the true character of the sexual organs in *P. omnivora* var. *Arecae*, above referred to, was correct (10).

Since that time five other species of Phytophthora have been described by the following authors:—Butler and Kulkarni (1); Pastur (2); Tanaka (Swada) (12); and Sherbakoff (13), in which the sexual organs are of the type found in *P. infestans*, the earliest described member of the group. The following is a list of all such species described up to the present:—

(1) *P. erythroseptica* Pethyb.
(2) *P. infestans* de Bary.
(3) *P. Phaseoli* Thaxt.
(4) *P. Arecae* (Colem.).
(5) *P. parasitica* Dast.
(6) *P. Colocasiae* Racib.
(7) *P. Allii* Saw.
(8) *P. Melongenae* Saw.
(9) *P. terrestria* Sherb.

It seems possible, judging from the published descriptions alone, that the last two species in this list may be identical, but this can only be decided by a careful comparison of pure cultures of the two.

The question arises as to whether the fungus which causes the disease of tomato plants described in the present paper is identical with any one of those enumerated above, or whether it must be regarded as a new species hitherto undescribed. From a careful study of the published descriptions we conclude that our fungus cannot be identical with any one of the above nine, but it is scarcely necessary to discuss the points of difference in detail here. The sporangia of the above-mentioned nine species, with the exception of *P. erythroseptica*, are all more or less distinctly papillate, while those of our fungus resemble those of the last-named species in being blunt or rounded at the apex.

Our fungus most nearly resembles *P. erythroseptica*, but differs from the latter in the size and colour of its sexual organs and also in its remarkable reluctance to produce sporangia and oospores in quantity. A long series of parallel cultures and infection experiments was carried out with these two fungi, into the details of which it is not necessary to enter here. It is

sufficient to state that the results showed conclusively that the two fungi are not identical; and we conclude that the tomato fungus is one which has hitherto not been described.[1]

Its diagnostic characters may be summed up briefly as follows :—

Phytophthora cryptogea sp. nov. Mycelio ramoso quoad partes recentiores eseptato vetustiores septato; conidiis plerumque inversipyriformibus 24-50μ × 17-30μ apicibus obtusis non-papillatis sympodialiter genitis; zoosporis 2-ciliatis 10-15μ diam.; oogoniis hyalinis flavescentibus pyriformibus 30μ diam.; antheridiis amphigynis hyalinis; oosporis sphaericis flavescentibus crasso episporio praeditis 25μ diam.

Hab. in radicis caulibusque vivis *Lycopersici esculenti* et *Petuniae* sp. in Hibernia.

VII.—The Disease in Plants other than the Tomato.

Petunia.—Some time after beginning the study of the Tomato disease we received specimens of Petunia seedlings suffering from a disease the symptoms of which were very similar to those observed in the Tomato plants.

Microscopic examination of the diseased tissues confirmed this similarity, for a Phytophthora-like fungus was present, bearing sporangia similar to those observed in the case of the Tomato.

The fungus was isolated from the Petunia in the same manner as was the one from the Tomato, and it was grown in pure culture. It was proved by infection experiments to be pathogenic not only to Petunia but also to Tomato, Aster, Wallflower, and *Gilia tricolor*.

In culture the fungus isolated from Petunia behaved exactly like that obtained from Tomato, and, like the latter, it produced sexual organs. These organs were similar in every respect in the two cases, and we conclude that *Phytophthora cryptogea* is the cause of the disease not only of Tomato plants but also of Petunias.

Aster.—About the same time diseased Asters were observed in a garden in the same locality as that from which the diseased Tomato plants were originally obtained. The root systems and the lower parts of the stems were

[1] While the present paper was being prepared for press we found that Mr. G. T. Spinks (14) had described a disease under the title "Damping-off and Collar Rot of Tomatoes," which is probably identical with the one we have been dealing with. The causative parasite appeared to be a species of Phytophthora, but it was not grown in pure culture, and no sexual organs were obtained. It was not therefore identified or described in detail.

more or less decayed; and microscopical examination revealed in them the presence of phycomycetous mycelium bearing Phytophthora-like sporangia.

The fungus was isolated and grown in pure culture. As far as the morphological characters of its mycelium and sporangia are concerned no differences could be seen between it and the fungus isolated from Tomato plants. It was proved to be pathogenic to Aster, Tomato, Petunia, Wallflower, and *Gilia tricolor*.

The finding of this fungus in Aster recalled the disease of this plant recently described by Robinson (9) and attributed by him to a species of Phytophthora. This author did not succeed in obtaining the sexual organs of the fungus in pure culture, and hence did not identify it or name it.

Mr. Robinson was good enough to supply us with a culture of his fungus, which, unfortunately, on its arrival was found to be contaminated with bacteria. We succeeded, however, in getting it pure, and we carried out a parallel series of cultures and infection experiments with it and with the strains isolated by us from Tomato, Petunia, and Aster.

It was found that Robinson's strain was pathogenic to exactly the same plants as the others were, and produced the same type of disease. But whereas in the case of the strains isolated by us from the Tomato and Petunia sexual organs were produced in pure culture, this was not the case with the strain isolated from Aster either by us or by Robinson.

A certain amount of doubt, therefore, must exist as to whether the fungus causing the Aster disease is absolutely identical with *P. cryptogea*. Judging from their very close similarity in other respects, however, and especially seeing that the formation of sporangium within sporangium (hitherto described for no other species) is common to both, it is clear that the two fungi are very closely allied if not absolutely identical. It is possible, too, that had the cultures been carried on for a more extended period, sexual organs would have developed in the course of time. Unfortunately only *P. cryptogea* from Tomato was carried over the period of eight months, during which the work was suspended, in a living condition.[1]

Cheiranthus.—Diseased Wallflowers were observed alongside of the Asters above referred to, showing similar symptoms. A similar fungus, bearing the same kind of sporangia, was found in the affected tissues. The fungus was not in this case isolated, but inoculation of healthy Wallflower plants with

[1] Mr. Brierley (Ann. App. Biology II, No. 4, Ap., 1916, p. 266) refers to tomato plants as succumbing to "Black Neck (*Phytophthora* sp. *omnivora*?)." In correspondence he informed us that he believed that this disease in tomatoes was identical with Robinson's Black Neck of Asters, and was due to the same parasite.

a pure culture of *P. cryptogea* from Tomato produced exactly the same type of disease.

Summing up, therefore, it may be stated that *P. cryptogea* is the cause of a disease of Tomato and Petunia plants, and in all probability causes a similar disease in Asters and Wallflowers.[1]

VIII.—Source of Infection and Control of the Disease.

All our observations point to the conclusion that the plants become infected through their roots from the soil. This is further borne out by the experience that when Tomato seeds were sown in the soil in which a diseased plant had been growing all the seedlings became affected with the Phytophthora disease when they were about two inches high. Seeds from the same source sown in sterile soil produced healthy seedlings.

At one of the nurseries visited it was found that it was the practice to raise Tomato seedlings in a compost made up of equal parts of virgin loam and leaf-mould, without the addition of any manure. The mould usually employed was derived from decomposed beech leaves (*Fagus sylvatica*).

Only small quantities of this loam and leaf-mould which had not previously been used were still available. Equal amounts of the two were mixed and filled into two seed pans. One of these was sterilised by exposure to live steam for a period of two hours at a time on three successive days, while the other was untreated. Tomato seeds were sown in each pan, and the result was that the seedlings which developed in the untreated mixture of loam and leaf-mould became diseased, while those in the sterilised mixture remained healthy. One of the diseased seedlings was removed and placed with its roots in sterile water, when the characteristic sporangia of the fungus developed.

It was suspected that the fungus might be present in the leaf-mould and not in the loam. An experiment was carried out to settle the matter, but the result was a negative one, for, in this case, no diseased seedlings arose either in the loam or the leaf-mould. This is probably explained by the fact that only a *very small* quantity of the leaf-mould and loam was still available for the trial, and in order to get enough material to fill even a three-inch pot the leaf-mould and loam had each to be diluted with a considerable amount of previously sterilised soil.

In this connexion it is at any rate interesting to observe that the fungus was proved to be pathogenic to beech. A beech-nut was planted in soil, and

[1] At the time of going to press we have received specimens of diseased cinerarias also attacked, apparently, by this fungus.

when the resulting seedling was about 4 inches high and quite healthy, it was inoculated near soil-level with a pure culture of the fungus. Within six days the seedling was dying, and microscopic examination showed the presence on it of the fungus, bearing its sporangia. *Nozemia fagi* is a well-known parasite of the beech, and it also attacks herbaceous plants such as Clarkia, &c. It would not be surprising therefore if *P. cryptogea* also turned out to be a parasite naturally occurring in beech-woods, and that it was carried through leaf-mould, employed in compost-making, to nurseries, there to become a serious pest to cultivated plants. This point, although at present a mere hypothesis, is well deserving of further study.

As regards the control of the "foot-rot" disease, it may in the first place be stated that this is one of those rather exceptional cases amongst plant diseases in which (as far as the Tomato is concerned at any rate) an actual cure of the individual may be effected by amputation of the attacked portion of the plant and treating the healthy portion as a cutting. The diseased portions removed should of course be destroyed by burning. Attention has already been drawn to this point; and, provided that the affected plants are old enough and are not in too advanced a stage of attack, this mode of treatment may be carried out without an undue amount of trouble and with the prospect of a reasonable degree of success. It is, perhaps, scarcely necessary to point out that the cuttings must not be planted in contaminated soil, otherwise there is serious risk of a recurrence of the trouble.

The precautionary measures which should be adopted to prevent the disease are sufficiently obvious. All diseased plants (if not treated as described above) should be destroyed by burning. All soil in which diseased plants have been growing should be discarded from the nursery. It could probably with safety be used as a top-dressing on permanent grass land. All pots, pans, boxes, &c., in which diseased seedlings have been raised should be thoroughly cleaned and disinfected or sterilised before being used again. A thorough cleansing and disinfection of glass-houses or frames in which diseased plants have been grown should also be carried out.

Seedlings should only be raised in non-contaminated soil. Experience has shown that it is not sufficient to rely on virgin loam and fresh leaf-mould for making the compost, because the fungus may already be present in one or both of these. The safest plan would be to sterilise thoroughly the compost before using it. Partial sterilisation, such as results from some of the modern methods of steaming employed in connexion with other diseases of the tomato, cucumber, &c., would probably not be sufficient.

IX.—Summary.

A disease of young Tomato plants is described in which the root system and the lower portion of the stem become involved in a rot leading ultimately to the death of the plant. The term "Tomato Foot-Rot" is suggested as appropriate for it.

A species of Phytophthora was isolated from the diseased tissues and was proved to be the cause of the disease.

The parasite was grown in pure cultures, and in these the development of sexual organs took place. They are the type first described in *Phytophthora erythroseptica* and *P. infestans.* The fungus is, therefore, a true Phytophthora, and not being identical with any one of the nine previously described members of this genus, is described as a new species under the name of *Phytophthora cryptogea.*

The same type of disease, caused by the same fungus, was found to occur naturally in Petunia; and it is extremely probable that the same fungus causes a similar disease in Aster and Cheiranthus

Artificial inoculations showed that the fungus was also pathogenic to Potato (*Solanum tuberosum*), *Gilia tricolor*, and *Fagus sylvatica*, but not to *Senecio vulgaris, Helianthus annuus*, or *Nicotiana affinis.*

The disease was found to be contracted from the soil. Oospores of the fungus probably hibernate there; but this point has not been demonstrated conclusively.

The disease can be prevented by raising Tomato plants in soil thoroughly sterilised by heat; and individual plants can be cured in many cases by amputating the diseased portion of the plant and treating the healthy remainder as a "cutting." Methods of controlling the disease are briefly outlined.

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XI.—Explanation of Plates.

Plate XLV.

Fig. 1. A typically diseased Tomato plant at a comparatively late stage of attack. The original roots are dead and decayed. A bunch of secondary adventitious roots has been developed higher up, but these have also become attacked by the fungus. The overground stem is shrivelled up to and just beyond the point of insertion of the lowermost leaf, which is dying. The leaflets of the leaf above this one are already beginning to show the characteristic rolling upwards and inwards of their margins. The remaining leaves are still normal.

Fig. 2. An infection experiment. The central plant (control) was wounded but not inoculated. It remained perfectly healthy. The two side plants were wounded and inoculated with a pure culture of *P. cryptogea*. Both became diseased. The one on the right has toppled over, and the shrunken base of the stem is clearly visible. The one on the left, although affected in a similar manner, was prevented from falling by being supported by a stake. The photograph was taken four days after inoculation.

Figs. 3–5. Photographs of the sexual organs of *P. cryptogea* developed in pure culture on Quaker Oat-agar. A thick-walled oospore is present in each case within the spherical portion of the oogonium, the funnel-shaped base of which is still within the antheridium. The hyphae bearing the oogonia and antheridia are not discernible. Figs. 3 and 5. × 540. Fig. 4 is the same as fig. 5. × 850.

Plate XLVI.

Cross-inoculation experiments with *P. cryptogea* on Tomato (fig. 1), Petunia (fig. 2), Aster (fig. 3), and Cheiranthus (fig. 4). In each case the normal plant in the right-hand pot served as a control, being wounded but not inoculated. The diseased plants in the three pots on the left in each series were wounded and inoculated in each case with pure cultures of the fungus isolated from Tomato, Aster, and Petunia respectively, from left to right.

Plate XLVII.

Fig. 1. Mycelium of *Phytophthora cryptogea* from a 30-day-old culture on maize meal agar. The slight constriction of the lateral branches at their points of origin is rather characteristic. × 510.

„ 2. Three immature sporangia from sporangiophores developed in water from mycelium in the affected portion of a young tomato plant artificially inoculated from a pure culture. × 510.

„ 3. More mature sporangia from the same source. The one on the left ripe, the one on the right about to liberate its zoospores. × 510.

„ 4. Sporangiophore and sporangia from the same source. The branching is sympodial, but the branches are unusually short. × 510.

Figs. 5 and 6. Sporangia produced by the fungus when growing on roots of Cheiranthus (after artificial inoculation). The upper sporangium in fig. 5 has commenced to develop a germ-tube. In fig. 6 the germ-tube is in a more advanced stage of growth. × 510.

Fig. 7. Two cases of the development of a second sporangium from within the base of the first formed one. × 510.

„ 8. Development of a third sporangium within two previously formed sporangia. × 510.

„ 9. Mycelium of *P. cryptogea* as developed occasionally from diseased portions of the host when submerged in water and also in pure culture, representing, possibly, abortive attempts at the production of sporangia or of sexual organs. × 510.

„ 10. Sporangium in which each zoospore-unit has developed a germ-tube without the liberation of free zoospores. × 840.

„ 11. Sexual organs of *P. cryptogea* from a 6-weeks-old pure culture on hard Quaker Oat-agar. × 740.

„ 12. Sexual organs of *P. erythroseptica* for comparison. × 740.

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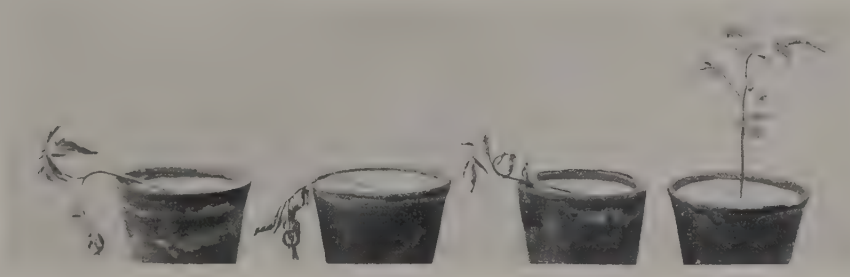

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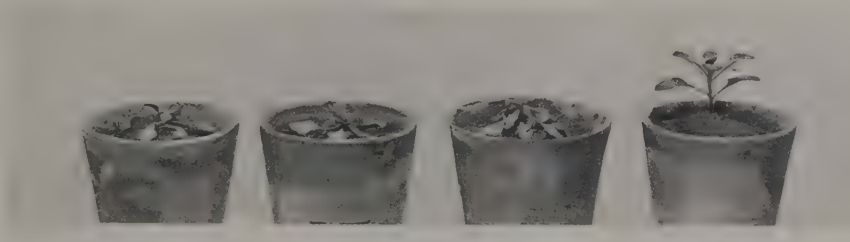

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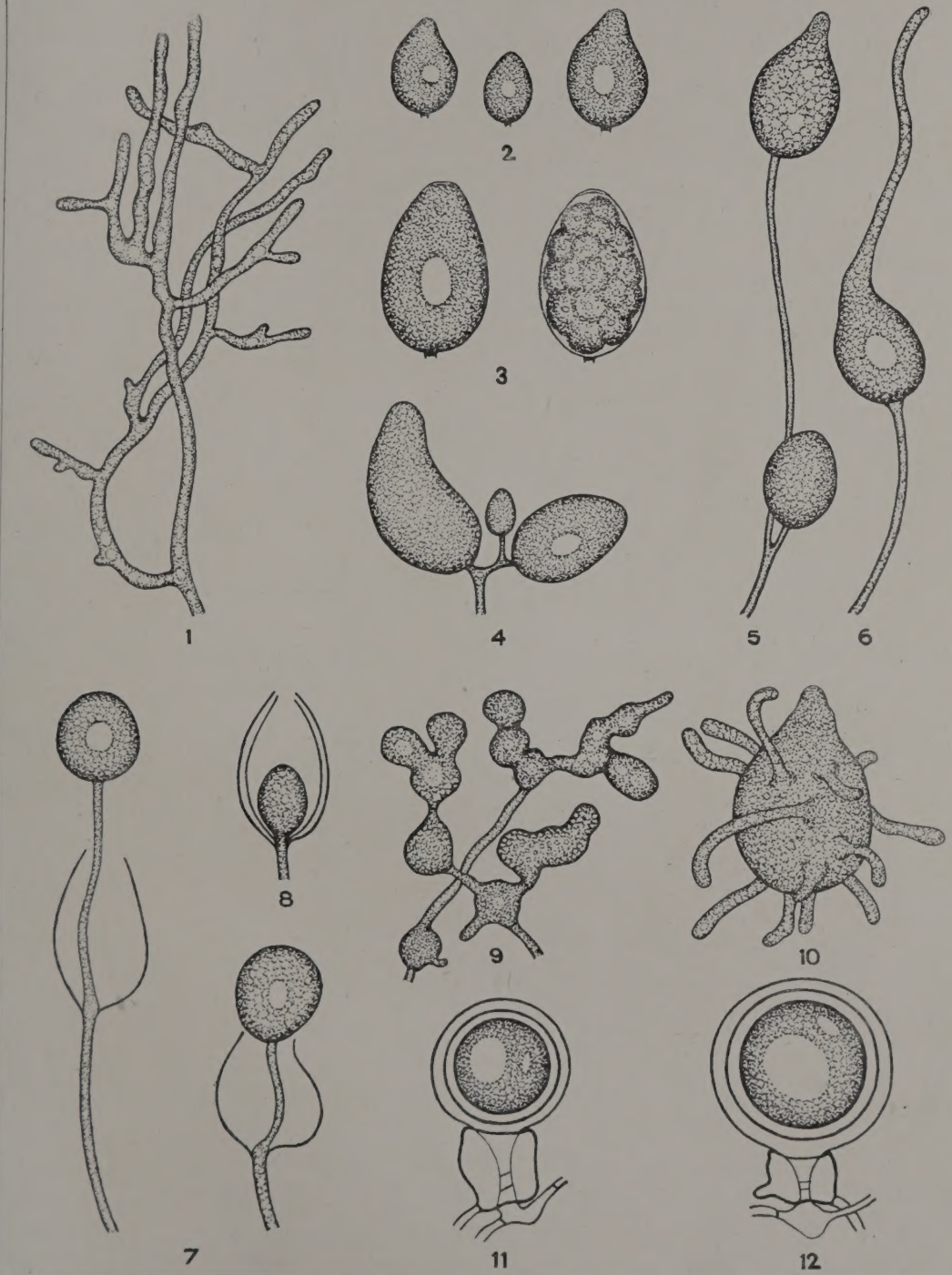

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